Introduction to PNAS special issue on evolutionary models of financial markets

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One of the longest debates in economics involves the existence of a rare Hominid "species" known as *Homo economicus*, the economic human. *H. economicus* is able to determine the optimal use of its resources to maximize its well-being as defined by the assumptions of neoclassical economics, leading to behavior that has come to be known as economic rationality. When interacting with other members of this species in market settings, such behavior leads to a magical outcome. The participants' self-interested efforts to exploit their disparate pieces of information aggregates, distills, and compresses their information into a single number: the price. And because no piece of information is left unused or uninterpreted in the process of price discovery, this market is deemed "efficient." Prices fully reflect all available information, as Eugene Fama concluded in his first articulation of the efficient markets hypothesis (1).

Modern financial theory and practice are built on the foundation of *H. economicus* and efficient markets. However, booms, busts, and financial crises have created stress fractures in that foundation, implying that investors are not fully rational, that markets are not infallible, and that their failure can be catastrophic for the global financial system. Behavioral economists, on the other hand, view investors and markets as fundamentally irrational and inefficient. From their perspective, *H. economicus* is a case study in cryptozoology, as relevant to scientific discourse as Sasquatch and the Loch Ness monster. Nevertheless, it is an empirical fact that markets behave well most of the time, and when they do break down, it is often for understandable and predictable reasons.

In recent years, the two sides of this debate have moved closer as more sophisticated models of investor behavior and macroeconomic dynamics have been developed to rationalize empirical anomalies, such as the equity risk premium, excess stock market volatility, the size premium, the closed-end fund puzzle, the apparent excess profitability of momentum and high-frequency trading strategies in the stock market, and the plethora of behavioral biases documented by experimentalists. State-dependent and nontime-additive utility functions, heterogeneity of preferences, asymmetric information and strategic behavior, Knightian uncertainty and ambiguity aversion, and other equilibrium models of capital market imperfections are just a few examples of theoretical innovations designed to address these anomalies.

However, in the wake of the 2008 financial crisis, economists were at a loss as to explain how their macroeconomic models failed so spectacularly in anticipating the shock waves from the financial sector that were triggered by the decline in United States residential real estate. In fact, many macromodels used by central banks around the world at the time did not even include the financial sector because the presumption was that financial markets would simply clear at the appropriate prices to facilitate the needs of the real economy. Some notable exceptions in which the financial sector has been shown to play a significant role in the real economy are the prescient models by Bernanke, Gertler, and Gilchrist (2) and Kiyotaki and Moore (3).

Consequently, a growing number of economists and financial industry professionals have begun looking to other disciplines for new insights, in an effort to develop a more parsimonious framework for capturing the complex dynamics exhibited by the real and financial sectors of the global economy over the last two decades. A new literature has emerged in which the standard economic assumptions are being reconsidered through the lens of evolution. The world's financial systems may well be complex, but they are certainly much less complex than the interactions that have evolved within the biological world, of which they are a proper subset.

This special issue of PNAS is intended to highlight this relatively new interdisciplinary field, featuring original joint research from collaborating biologists and financial economists on the interplay between evolutionary theory and market dynamics. The aim of this research is not to debunk traditional financial theories, but rather to complement existing research and attempt

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to reconcile the apparent gap between theoretical ideals and empirical realities. Given that financial economics is based so heavily on empirical observation, the synergies with evolutionary theory—which emerged from Charles Darwin's careful study of Galápagos flora and fauna and other studies—run deep. This program is intended to improve our models rather than simply assume away or ignore the apparent inefficiencies and irrationality contained in financial data. The application of principles and techniques from evolutionary biology and associated disciplines, like ethology and ecology, may provide a key to unlocking long-standing puzzles within these disciplines. Our goal in publishing this special issue is to disseminate these ideas to a broader audience, and to encourage greater collaboration among ecologists, economists, evolutionary biologists, regulators, and finance professionals.

We motivate this ambitious initiative with an analogy. The brilliant evolutionary insights of Darwin and others have revolutionized our understanding of the world. Darwin was impressed by the "tangled bank" of elaborate forms that emerged from the undirected processes of evolution to produce the complexity of the biological world. Through continuous innovation coupled with the deceptively simple filter known as natural selection, the characteristics of species and their interactions change in response to changing environments. However, evolution is not limited only to the biological world. Wherever the evolutionary forces of reproduction, variation, and selection exist—as they do in financial markets—evolutionary consequences will follow. There are of course major differences as well between the nature of the evolutionary process in ecological and economic contexts, largely influenced by the relative importance of top-down control, and the degree to which predictive models and long-term planning can be invoked. These are, however, differences of degree.

There are profound similarities between financial systems and the biosphere. Both are complex adaptive systems in which individual agents act to enhance their own interests and objectives, leading to self-organization and emergent features. In viewing global financial markets as comprising a complex-adaptive biological system, researchers in this area intend to develop more effective models to understand these systems. This is not only of theoretical interest, but also has the practical aim to promote economic growth while maintaining financial stability, with the ultimate goal of allocating resources more efficiently through better financial methods.

Evolution is about short-term, relative optimality with respect to other participants in the system. In the biosphere, natural selection acts to improve reproductive success relative to the benchmark of other genomes, within and across species. Evolutionary change can thus be thought of in terms of differential fitness: that is, small differences in reproductive rates between individuals over time leading to large differences in populations. Even the very mechanisms of evolution—including those that generate new variation—are subject to constant modification. In the financial world, the evolutionary forces of mutation, recombination, reproduction, and selection often work on financial institutions and market participants through direct competition, finance "red in tooth and claw." Financial concepts and strategies thus reproduce themselves through cultural transmission and adoption based on their success in the marketplace. These strategies undergo variation through financial innovation, analogous to mutation or genetic recombination in a biological system, but take place at the level of information and abstract thought in financial contexts. It is "survival of the richest."

To a large extent, evolution is also about interaction with the unknown, because the scope of possible changes in the environment is so immense. The interplay between exploration (through which new solutions are tested) and exploitation (through which the best solutions are implemented) is characteristic not only of biological evolution via natural selection, but also of the way investors, firms, and financial institutions must divide their time and effort to survive. This tradeoff underscores the importance of maintaining diversity and heterogeneity in financial markets, allowing enough exploration, via financial innovation, to produce this essential diversity. As in purely biological systems, the balance between exploration and exploitation will depend upon context, and upon endogenous as well as exogenous sources of variability and uncertainty.

Additionally, evolution is able to answer many fundamental questions about the nature of risk. No form of exploration is entirely without risk, whether in the biosphere or in the financial world. Species have evolved behaviors to manage risk successfully, whether in their foraging strategies, their methods to capture prey, their methods to evade predation, or their mating strategies. Genomes will also evolve different strategies when faced with idiosyncratic versus systemic risk in their environment. Risk-aversion and risk-seeking behaviors can be understood as the consequence of environmental pressures on the evolutionary history of the organism. A similar dynamic holds for agents in model evolutionary systems, where a diverse collection of economic behaviors, including cooperation, can be generated from different factors in the environment.

The collective actions of individual agents pursuing their evolutionary self-interest, whether biological or financial, often have unpredictable consequences at the level of the entire system. These consequences can then feed back to the level of individual actions. The results should come as no surprise: These emergent phenomena may lead to systemic crises and collapses, from an explosion in pest species and pathogens to bank panics and global financial crises.

By studying how and to what degree evolution has made biological systems more robust, we may be able to develop new approaches to financial regulation (4). A robust and sustainable system depends on homeostasis, the maintenance of a stable state; homeorhesis, the maintenance of a stable dynamic trajectory; or more generally, the structural stability of systems dynamics. Homeostasis and homeorhesis both require feedback mechanisms strong enough to sustain desirable patterns, but not so strong as to create destabilizing oscillations or chaos. When these feedback loops are too weak or too slow, pathologies arise, such as Cheyne-Stokes breathing. When feedback loops are too strong, we also observe pathologies, such as autoimmune responses and cytokine storms. Similarly, when the pace of financial innovation outstrips regulation, the financial system can begin to break down, as during the financial crisis of 2007 to 2008. However, regulatory responses that are too strong can lead to economic outcomes that are equally undesirable, such as chronic shortages of goods and diminished investment in research.

The evolutionary lens provides a natural way to introduce biological concepts into financial and economic analysis. As the evolutionary biologist Theodosius Dobzhansky said, "Nothing in biology makes sense except in the light of evolution" (5). The same may hold for the financial world. Phenomena that have been difficult to analyze within a traditional economic framework, such as growth, size, scale, self-organization, the lifecycle of products and industries, bull/bear market cycles, and the rate of variation or

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innovation within a system, are all subject to evolutionary forces, whether they take place in the Petri dish or on the trading floor. Biological experiments thus may be able to directly inform economic insights, and market behavior may be able to shed light on evolutionary mysteries in the biological world.

Most importantly, evolutionary insights into investor behavior and financial market dynamics permit a natural alternative to the concept of the efficient markets hypothesis that currently forms the cornerstone of modern financial thinking. Rather than prices reflecting all available information to investors—among whom irrational behavior is arbitraged away to someone else's profit—under the adaptive markets hypothesis (6, 7), markets can be considered as evolutionarily adaptive systems in which the degree of efficiency is related to environmental factors characterizing the local financial ecology, such as the population structure of investors, the magnitude of available profit opportunities, and the historical evolution of their trading strategies. The adaptive markets hypothesis thus provides an explanation for why suboptimal investment strategies may persist in a market over time, and why market conditions may change over relatively brief periods.

Finally, the evolutionary view of financial systems recognizes that these systems are analogous to biological systems in more than name. Modern ecological models analyze the interactions of species in different niches with each other and with the environment in terms of the stocks and flows of its fundamental building blocks, matter and energy. Just as ecosystem ecology is focused on the cycling of crucial elements like carbon, nitrogen, and phosphorus, financial-system ecology should be focused on the cycling of crucial elements, like financial liquidity, volatility, credit, and innovation through the global economic system. The trophic webs and networks that characterize ecological thinking have clear parallels in the increasingly networked world of modern finance.

This rich tapestry of evolutionary thinking is evident among the articles in this special issue. Amir et al. (8) explore the development of trading strategies in an evolutionary finance setting in their paper, "Evolution in pecunia," a play on the common specification of an experiment as occurring in vitro or in silico. In this paper, financial markets are analytically modeled as analogous to evolving biological systems in a stochastically dynamic game theoretic framework, using only variables based on objectively observable market data. This evolution does not take place at the level of the individual, but at the level of the trading strategy, all investment in a single "fixed-mix" strategy treated as the equivalent of a biological species, competing for capital and survival. This model introduces an innovation in which dividends from assets are not exogenous, but rather, increase with the amount of wealth invested in an asset, in a stylized version of dividends in a production economy. Amir et al. find that a positive feedback loop, in which more investment in an asset leads to higher dividends, in turn leading to larger investments, is avoided. Instead, an evolutionarily stable investment strategy is identified, which characterizes a locally stable equilibrium state. This is indicative that evolutionary dynamics in the marketplace are still able to produce stable prices in the absence of large exogenous shocks.

Scholl et al. (9), in "How market ecology explains market malfunction," consider an agent-based "toy" model of a market consisting of three species-like types of strategies—value investors, trend followers, and noise traders—in which the wealth invested in a financial strategy is analogous to the species' abundance. In this model, the average returns of a strategy are strongly density-dependent, to use the ecological term; they depend on the wealth invested in each strategy (not merely their own) at any given time. This market ecology shows a slow evolution toward an efficient equilibrium where all three strategies make the same average returns, but the statistical uncertainty in profitability makes this noisy, causing bursts of volatility, and the market spends extended periods of time away from perfect efficiency, where prices deviate from fundamental values. Concepts from ecology, such as the community matrix of species interaction and trophic levels in food webs, have been innovatively applied within this model, showing that these strategies can be competitive, mutualistic, or even similar to cannibalism, depending on the wealth invested in each. The rich dynamics of this toy market ecology thus show how market inefficiencies and "malfunctions" may spontaneously occur.

Musciotto et al. (10) focus the evolutionary lens on the effects of innovation and regulatory change on the financial markets in "High-frequency trading and networked markets." During the last 20 years, a mixture of technological innovation and regulatory requirements has promoted the diffusion of market fragmentation and high-frequency trading across the global financial system. The traditional market ecology of participants and professionals has quickly evolved into a complex network of interactions among market participants, including firms of high-frequency traders, characterized by heterogeneous time scales of more than eight orders of magnitude. Musciotto et al. show that transactions between specific pairs of market members are systematically under- or overexpressed through time. This implies that liquidity provision to members of modern stock markets is not unconditional, but rather that it has statistically detectable preferences or avoidances that extend over periods of months. The Musciotto et al. paper analyzes datasets from the electronic order book of the London Stock Exchange and the Stockholm venue of the NASDAQ-OMX market, recorded between 2004 and 2006, 2010 to 2011, and 2018. Rather than diminishing with the advent of high-frequency trading and market fragmentation, these relationships were instead enhanced, increasing in number and persistence in this new financial environment.

Koduri and Lo's "The origin of cooperation" develops a mathematical theory of how natural selection operates in the presence of a generic interaction among replicating units (11). Two types of interacting individuals reproduce under random environmental conditions in this evolutionary model. With the addition of interaction, natural selection does more than seek to maximize the number of offspring of each type. Not only does the evolutionarily dominant behavior maximize the number of offspring of each type, it also minimizes the correlation between the fecundity of each type, driving it toward −1, perfect anticorrelation. Koduri and Lo argue that correlation is a mechanism by which evolution can select for cooperation. This mechanism is distinct from standard biological explanations for the evolution of cooperation—such as kin selection, group selection, or reciprocity—relying only on natural selection without recourse to notions of evolutionary stability. Several examples illustrate how correlation can be used to explain the evolution of cooperation, including through specialization, sacrifice, and coordination.

In "Moonshots, investment booms, and selection bias in the transmission of cultural traits," Hirshleifer and Plotkin (12) discuss the effects of selection on the transmission of information about the financial success of firms. Evolution here is driven not only by the differential copying of successful traits, but also by cognitive reasoning about which traits are more likely to succeed. In their model, each firm makes the decision to adopt or reject a project with two possible payoffs, one positive and one negative. Before

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making its decision, however, it observes the payoffs received by past firms. This model applies two selection filters to this observation. The first models the tendency for firms to believe that large payoffs to other firms are more significant than small successes or failures. The second models the phenomenon known as selection neglect, the failure to adjust for observational bias. There is thus a probability that the observed outcome will be censored, especially if the payoff was negative. The failure to account for biased censorship causes firms to become overly optimistic, leading to irrational booms in the adoption of innovation, risk-taking behavior, and investment. These cultural evolutionary changes are analyzed using Price's equation, borrowed from population genetics, to decompose the effects of mutation pressure and evolutionary selection. Hirshleifer and Plotkin's model thus provides a new explanation for investment booms, "merger manias," and waves of technological and financial innovation.

Another long-standing puzzle in economics regards the equity premium, the observation that people invest far less in equities (i.e., the stock market) than is implied by other measures of risk aversion. Robson and Orr's "Evolved attitudes to risk and the demand for equity" argues that the risk preferences at play in this puzzle were at least partly shaped by human evolutionary history (13). The standard economic treatment of risk preference has difficulty explaining this phenomenon. However, a simple evolutionary model shows that natural selection will select for a greater aversion to shared aggregate risk than to personal idiosyncratic risk. Robson and Orr apply this model to show that an evolutionary aversion to aggregate risk may explain the equity premium puzzle in both a static model of portfolio choice and a dynamic model that allows for intertemporal tradeoffs. Since the stock market involves aggregate risk rather than idiosyncratic risk, this helps to resolve the puzzle.

Akçay and Hirshleifer's "Social finance as cultural evolution, transmission bias, and market dynamics" outlines a new paradigm for studying the cultural evolutionary system that animates the thoughts and behaviors of financial market participants, social finance (14). In this paradigm, cultural financial traits, such as information signals, investor beliefs, trading strategies, and folk economic models, compete to survive in the population, but are modified in transmission by social biases [as in Hirshleifer and Plotkin (12)]. These cumulative evolutionary processes help to shape market outcomes, which subsequently exert feedback into the relative success or failure of financial traits. The social finance paradigm allows these traits to become endogenized in Akçay and Hirshleifer's (14) treatment, while the socially biased transmission of traits in social finance models is able to naturally accommodate psychological bias, information asymmetry, and social network structure. Social finance models have especially been able to capture behavior at the extreme ends of the time scales of financial dynamics, characterized by its heterogeneous range of frequencies.

Burnham and Travisano's "The landscape of innovation in bacteria, battleships, and beyond" uses the evolutionary concept of the "adaptive landscape," the multidimensional relationship between organismal form and evolutionary outcome, to characterize environments that increase the speed and magnitude of innovation (15). Burnham and Travisano compare two case studies: Richard Lenski's ongoing long-term evolution experiment that follows the bacterium *Escherichia coli* through thousands of generations of biological selection and adaptation, and the naval arms race in battleship design in the 19th and 20th centuries. The authors contrast incremental evolution as movement toward a local "peak" in the adaptive landscape, characterized by harsh environments and hard competition, versus radical evolution, involving changes along multiple dimensions in the adaptive landscape, in an environment characterized by soft competition. They apply this framework to innovation in portfolio management, comparing the difficult environment of active investing to the radical evolution of passive investing. Burnham and Travisano conclude that to shape the adaptive landscape to favor innovation, the better approach may be to soften competition.

Romano and Levin's "Sunsetting as an adaptive strategy" examines the legislative mechanism known as "sunsetting" through its parallels in evolutionary biology, in which analogous phenomena have evolved to enhance the ability of organisms to adapt to changing environments (16). With sunsetting, after a fixed time span, legislation and its implementing regulation "sets," and it must be reenacted to remain in force. Analogous biological phenomena like apoptosis, programmed cell death, are a natural part of the growth and development of an organism. Sunsetting does not mean simply discarding or reenacting existing regulations, but revisiting them and improving them, much as mutation and recombination do in the evolutionary process. Sunsetting has an obvious place as a mechanism in crisis-driven financial legislation. Major legislation following a financial crisis can be hazardous, because information regarding the fundamental causes of the crisis is typically scarce. At the same time, financial markets are dynamic, while crisis-driven legislation is "sticky," which can undermine the efficacy of new regulation. As a result, it is foreseeable that such legislation will contain at least some provisions that will have consequences that are not well understood, or even knowable. Romano and Levin thus advocate the use of sunsetting as a mechanism for mitigating the potentially adverse consequences of crisis-driven financial legislation.

In the past several decades, there has been an increasingly rich literature at the interface between ecology and evolution on the one hand, and economics and finance on the other. The fact that these disciplines all deal with complex adaptive systems means that many of the issues confronted—finding the best solutions in the face of uncertainty, scaling from the microscopic to the macroscopic, the emergence of patterns at higher level from interactions among agents at lower levels, and the conflicts that arise between the interests of agents and the interests of the collectives to which they belong—are similar across these subjects, and hence the insights gained from multiple perspectives lead to fertile cross-pollination. The papers in this issue explore the insights that an evolutionary perspective can bring to financial regulation, and we hope and expect that they will catalyze even greater interdisciplinary advances, and stimulate others to turn their attentions to these fascinating approaches.

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